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Temperature-dependent development of *Cnaphalocrocis medinalis* Guenée (Lepidoptera: Pyralidae) and their validation in semi-field condition

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ABSTRACT

The developmental time and survival of the immature stages of *Cnaphalocrocis medinalis* Guenée were studied at nine constant temperatures (15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5, and 35 °C), 40 ± 10% relative humidity, and a 16:8 h light:dark cycle. The total developmental time decreased with increasing temperature between 15 (115.6 days) and 32.5 °C (20.9 days), but increased above 32.5 °C. The relationship between the developmental rate and temperature was fitted by a linear model and three nonlinear developmental rate models (Logan 6, Briere 1, and Shi et al.). The nonlinear shape of temperature-dependent development was best described by the Briere 1 model ($r^2 = 0.99$), and this was supported by statistical information criteria. The total mortality of immature *C. medinalis* was lowest at 25 °C (67.2%) and highest at 35 °C (98.1%). The distribution of the developmental times of each stage was described by the two-parameter Weibull distribution equation ($r^2 = 0.84–0.96$). The predicted date for the cumulative 50% moth emergence was within a variation of one day using the Briere 1 model. The temperature-dependent developmental models for *C. medinalis* could be applied to determine an optimal management strategy for *C. medinalis* in paddy fields, and will be helpful in developing a full-cycle phenology model for *C. medinalis*.

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Introduction

The rice leaf folder, *Cnaphalocrocis medinalis*, is one of the most destructive insect pests of rice, *Oryza sativa* L., growing in Africa, Asia, Australia, and Oceania (Wada, 1979; Khan et al., 1988; Park et al., 2010a, 2010b). *C. medinalis* was considered a minor pest before the spread of high-yielding varieties of rice and double-cropping areas (Loevinsohn et al., 1993). Thereafter, however, it caused serious damage to rice development and production (Alvi et al., 2003; Padmavathi et al., 2013). The *C. medinalis* population has been managed by chemical control, but insecticide resistance and sporadic resurgence of *C. medinalis* have occurred within the rice cropping area (Park et al., 2010a, 2010b; Zheng et al., 2011).

The first- and second-instar larvae rarely fold leaves because they lack the physical strength to manipulate the leaf blades. In contrast, third- to fifth-instar larvae are typically able to fold leaves. Folds are created when a larva folds a leaf blade with silk strands and scratches

the inside of the folded leaf. This feeding behavior causes a reduction in photosynthetic availability and chlorophyll loss, and alters the water balance of the rice leaf until the leaf becomes withered (Islam and Karim, 1997). The damaged rice plants are thereby exposed to bacterial and fungal infection. Furthermore, the rice sheath becomes rotten, and heading and ripening are also suppressed, leading to a massive loss of rice production. A single leaf is not sufficient to support complete larval development, and therefore one larva will destroy several leaves during its development (Islam and Karim, 1997; Litsinger et al., 2006; Padmavathi et al., 2013).

Reports of the occurrence of *C. medinalis* have been highly variable by location and by year (Kawazu et al., 2005; Park et al., 2010a, 2010b). The colonization and damage caused by *C. medinalis* occur during the rice growing season, but the period of heaviest infestation occurs during the reproductive and ripening stages, leading to a greater economic loss of rice production (Wada et al., 1980; Alvi et al., 2003; Padmavathi et al., 2013). The damage caused by *C. medinalis* has increased in China since 2003, and the occurrence of *C. medinalis* populations has increased in Korea since that time. It is believed that this pattern is attributable to *C. medinalis* using jet streams to migrate from China to Korea and Japan from June to July, as is the case with the rice planthopper, *Nilaparvata lugens* (Stål) (Kawazu et al., 2005). Although the effects of the rice growing stage and temperature on the development of immature *C. medinalis* (Wada and Kobayashi, 1980), as well

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as the molecular mechanisms underlying the biological characteristics of *C. medinalis* (Li et al., 2012), were studied, a model that evaluated the relationship between the temperature and the development of immature *C. medinalis* was not investigated in detail.

Temperature is an important abiotic factor that regulates the development, phenology, and population dynamics of insects (Zahiri et al., 2010; Han et al., 2013; Wang et al., 2013). Understanding the relationship between the temperature and the developmental rates of a target pest is important in predicting the seasonal occurrence of the species and to establish environment-friendly pest management strategies (Kim and Lee, 2010; Notter-Hausmann and Dorn, 2010; Ahn et al., 2012). Therefore, an understanding of this relationship is needed to develop a reliable temperature-dependent developmental model for *C. medinalis* in order to formulate effective pest management plans.

Materials and methods

Insect colony

Cnaphalocrocis medinalis larvae and adults were originally collected from two locations in Yeongkwang (35°28'N 126°51'E) and Kwangyang (34°96'N 127°69'E), Jeonnam, Korea, in 2004. Adults were collected with sweep nets during the peak adult density at each site and transferred onto rice plants within a plastic container (width × length × height, 45 × 44 × 66 cm). For obtaining *C. medinalis* larvae, folded rice leaves were collected and transferred into the icebox. The larvae were carefully selected from the folded leaves in the laboratory because some larvae were contaminated by microbes or attacked by parasitoids. Colonies of *C. medinalis* were maintained in the laboratory at 25 ± 2 °C, 40 ± 10% relative humidity, and a 16:8 h light:dark cycle following the mass rearing methods of Shono and Hirano (1989) and Park et al. (2006).

Experimental procedure of development

To obtain a cohort of *C. medinalis* eggs, approximately five *C. medinalis* females and males were transferred from the stock culture to a plastic container (diameter × height, 9.0 × 8.0 cm; SPL Life Sciences). A piece of water-saturated cotton was placed in the container to maintain the relative humidity, and the *C. medinalis* adults were provided with sugar solution (10%) as a food source. The mated females were allowed to lay

eggs for 12 h, and one egg was selected randomly from the egg stock and transferred to a Petri dish (diameter × height, 5.0 × 2.0 cm). After the *C. medinalis* eggs hatched, fresh rice leaves (var. Chucheong) were supplied to young larvae (1st to 3rd instars), whereas older larvae (4th to 6th instars) were supplied with leaf blades as a food source because the development of *C. medinalis* larvae is influenced by the growing stage of rice (Heong, 1990).

The developmental times of *C. medinalis* from egg to adult emergence were investigated at temperatures of 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5, and 35 °C. Sample sizes were more than 100 eggs per treatment. Observations were made at 12-h intervals with the naked eye and/or with a binocular microscope (×16) to distinguish the larval instars. Larval instar was identified by head capsule width and body length. The developmental time of each immature stage was recorded.

Analysis of developmental data

The developmental times of each life stage of *C. medinalis* were analyzed using the PROC GLM in SAS (SAS Institute, 2002). The statistical differences of developmental duration among the temperatures tested were evaluated by one-way analysis of variance. Significant differences among multiple means were determined by using Tukey's studentized range test.

The relationship between developmental rates (1/developmental periods) and temperatures was analyzed with linear and nonlinear functions. The nonlinear functions proposed by Logan et al. (1976), Briere et al. (1999), and Shi et al. (2011) were applied to estimate the parameters. The equations are as follows:

$$r(T) = \Psi \left(e^{\rho T} - e^{\rho T_M - (T_M - T)/\Delta T^d} \right) \quad (1)$$

$$r(T) = aT(T - T_L)(T_M - T)^{1/2} \quad (2)$$

$$r(T) = m(T - T_L) \left(1 - e^{(K(T - T_M))} \right) \quad (3)$$

Eq. (1) is the Logan 6 model, where $r(T)$ is developmental rate at each temperature, ψ is the maximum development rate, ρ is a constant defining the rate of optimal temperature, T is the tested temperature (°C), T_M is the higher developmental threshold, and ΔT is

Table 1
Developmental time (days) (mean ± SEM) and mortality (%) for immature stages of *Cnaphalocrocis medinalis*.

Temperature (°C)	Life stage											
	Egg	1st larva	2nd	3rd	4th	5th	6th	Larval period	Prepupa	Pupa	Total immature	
15	DT	14.5 ± 0.17	17.3 ± 0.65	11.7 ± 0.66	9.7 ± 0.32	10.0 ± 0.32	12.9 ± 0.49	14.2 ± 0.60	78.8 ± 2.83	4.4 ± 0.31	35.4 ± 0.58	115.6 ± 3.51
	M	24.1 (88)a	25.0 (66)a	51.5 (32)a	25.0 (24)a	20.8 (19)a	15.8 (16)a	0.0 (16)a	81.8 (16)a	0.0 (13)a	0.0 (13)a	88.8 (13)a
17.5	DT	12.5 ± 0.11	11.1 ± 0.39	9.9 ± 0.49	7.1 ± 0.15	7.5 ± 0.36	9.0 ± 0.36	10.4 ± 0.22	55.00 ± 1.19	4.1 ± 0.26	26.1 ± 0.58	92.9 ± 1.40
	M	28.8 (125)b	28.8 (89)b	38.2 (55)b	21.8 (43)b	11.6 (38)b	0.0 (38)b	7.9 (35)b	72.0 (35)b	0.0 (35)a	0.0 (35)b	81.8 (32)b
20	DT	9.2 ± 0.15	6.2 ± 0.17	4.5 ± 0.11	4.8 ± 0.29	5.7 ± 0.45	6.2 ± 0.35	6.3 ± 0.44	33.70 ± 0.44	3.0 ± 0.01	15.0 ± 0.32	53.1 ± 1.12
	M	33.0 (77)c	33.8 (51)c	33.3 (34)c	5.9 (32)c	9.3 (29)c	3.4 (28)c	14.3 (24)c	68.8 (24)c	0.0 (24)b	0.0 (24)c	79.1 (24)c
22.5	DT	5.9 ± 0.05	4.7 ± 0.11	4.5 ± 0.27	4.0 ± 0.24	4.6 ± 0.35	5.3 ± 0.28	5.4 ± 0.23	28.50 ± 0.96	2.5 ± 0.11	11.6 ± 0.14	41.4 ± 0.64
	M	38.1 (95)d	38.9 (58)c	32.8 (39)cd	5.1 (37)cd	5.5 (35)d	0.0 (35)c	0.0 (35)cd	63.2 (35)cd	0.0 (35)c	0.0 (35)d	78.6 (33)d
25	DT	4.8 ± 0.05	4.1 ± 0.05	3.1 ± 0.10	2.7 ± 0.15	2.9 ± 0.14	3.5 ± 0.26	4.4 ± 0.12	20.70 ± 0.46	1.9 ± 0.02	8.2 ± 0.14	33.3 ± 0.36
	M	23.2 (89)e	23.6 (68)d	14.7 (58)d	10.3 (52)d	3.8 (50)e	6.0 (47)d	4.3 (45)de	49.4 (45)de	4.4 (43)d	4.7 (41)e	67.2 (38)e
27.5	DT	3.8 ± 0.03	3.1 ± 0.07	2.2 ± 0.09	2.5 ± 0.16	2.5 ± 0.12	3.0 ± 0.17	3.2 ± 0.15	16.50 ± 0.15	1.8 ± 0.07	5.9 ± 0.07	25.7 ± 0.43
	M	43.4 (183)f	43.7 (103)e	6.8 (96)e	7.3 (89)e	10.1 (80)e	6.3 (75)d	6.7 (70)ef	61.7 (70)ef	5.7 (66)d	0.0 (66)f	80.2 (64)f
30	DT	3.5 ± 0.04	2.9 ± 0.06	2.5 ± 0.16	2.2 ± 0.19	2.7 ± 0.15	3.0 ± 0.15	3.0 ± 0.20	16.30 ± 0.20	1.8 ± 0.08	5.5 ± 0.11	23.8 ± 0.57
	M	20.6 (94)g	21.3 (74)e	20.3 (59)e	15.3 (50)e	4.0 (48)e	0.0 (48)d	6.3 (45)f	52.1 (45)f	6.7 (42)d	4.8 (40)f	68.9 (37)f
32.5	DT	3.1 ± 0.01	2.9 ± 0.07	1.9 ± 0.15	2.2 ± 0.15	2.6 ± 0.21	3.2 ± 0.20	3.2 ± 0.24	16.0 ± 0.24	1.9 ± 0.10	5.4 ± 0.15	20.9 ± 0.69
	M	30.4 (110)h	30.9 (76)e	53.9 (35)e	31.4 (24)e	8.3 (22)e	13.6 (19)d	0.0 (19)ef	82.7 (19)ef	26.3 (14)d	50.0 (7)f	96.9 (5)f
35	DT	2.8 ± 0.02	2.7 ± 0.05	2.0 ± 0.05	2.3 ± 0.06	2.4 ± 0.06	3.0 ± 0.09	3.5 ± 0.24	15.9 ± 0.24	1.9 ± 0.04	5.7 ± 0.11	21.6 ± 0.62
	M	22.0 (243)h	22.2 (189)e	33.3 (126)e	21.4 (99)e	29.3 (70)e	12.9 (61)d	26.2 (45)ef	81.5 (45)ef	26.7 (33)d	45.5 (18)f	98.1 (6)f

Numbers in the parentheses are numbers of live individuals at each developmental stage. DT = developmental time (day), M = mortality (%).

Means followed by the same letter within a column are not significantly different ($P < 0.05$, Tukey studentized range test, Egg: $F_{8, 1095} = 3488.12$, $P < 0.0001$; 1st: $F_{8, 479} = 676.34$, $P < 0.0001$; 2nd: $F_{8, 357} = 231.98$, $P < 0.0001$; 3rd: $F_{8, 325} = 139.86$, $P < 0.0001$; 4th: $F_{8, 350} = 100.20$, $P < 0.0001$; 5th: $F_{8, 260} = 150.06$, $P < 0.0001$; 6th: $F_{8, 122} = 178.79$, $P < 0.0001$; prepupa: $F_{8, 228} = 72.69$, $P < 0.0001$; pupa: $F_{8, 230} = 1187.95$, $P < 0.0001$; total immature: $F_{8, 179} = 835.24$, $P < 0.0001$).

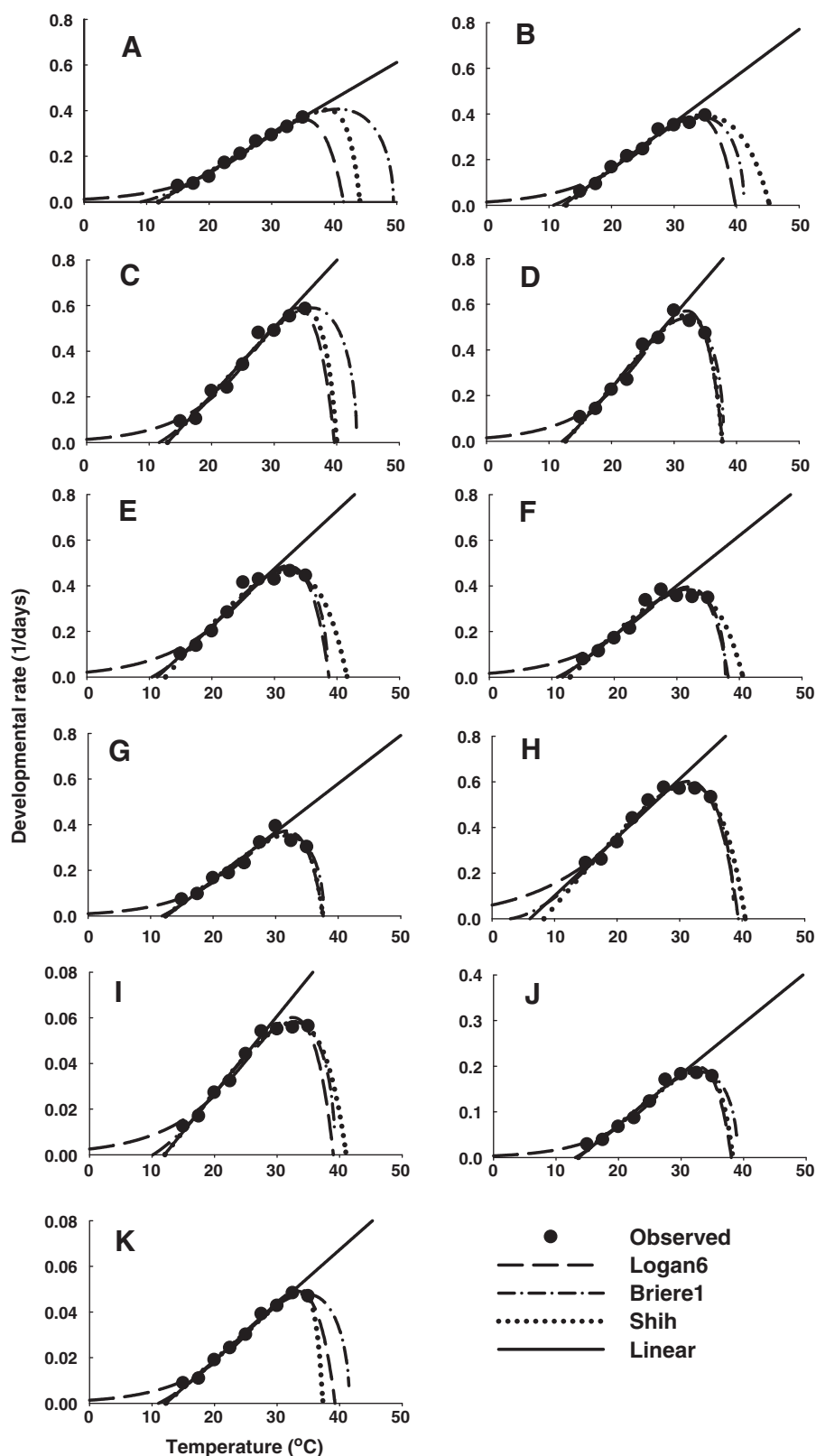


Fig. 1. Linear and three nonlinear functions fit to the data of developmental rates (day^{-1}) of *Cnaphalocrocis medinalis*: (A) for the eggs, (B) for the 1st instar larva, (C) for the 2nd instar larva, (D) for the 3rd instar larva, (E) for the 4th instar larva, (F) for the 5th instar larva, (G) for the 6th instar larva, (H) for the larva period, (I) for the prepupa, (J) for the pupa, and (K) for the total immature.

the temperature range over which physiological action induces important effect of development. Eq. (2) is the Briere 1 model. Here, T and T_M are as in the Logan 6 model, T_L is the lower developmental threshold, and a is a parameter of the equation. Eq. (3) is a

performance model of Shi et al. In this model, T , T_L , and T_M are as in the other models; m and K are parameters to be fitted.

The parameter values of the linear and nonlinear functions were estimated using the PROC REG and the PROC NLIN in SAS

Table 2

Lower developmental threshold (°C) and thermal constant (DD) estimated from the linear regression for *Cnaphalocrocis medinalis*.

Life stage	Regression equation	r ²	Lower developmental threshold (LT) (°C)	Thermal constant (DD)
Egg	0.0162x – 0.1949 (0.0015) (0.0340)	0.964	11.965	61.387
1st larva	0.0213x – 0.2680 (0.0014) (0.0308)	0.983	12.565	46.882
2nd	0.0305x – 0.4006 (0.0038) (0.0839)	0.939	13.136	32.786
3rd	0.0300x – 0.3684 (0.0029) (0.0647)	0.962	12.271	33.311
4th	0.0291x – 0.3576 (0.0028) (0.0623)	0.962	12.284	34.352
5th	0.0253x – 0.3265 (0.0024) (0.0529)	0.964	12.789	39.169
6th	0.0191x – 0.2279 (0.0018) (0.0410)	0.962	11.901	52.219
Larval period	0.0034x – 0.0404 (0.0048) (0.0002)	0.983	11.982	296.736
Prepupa	0.0289x – 0.2193 (0.0023) (0.0515)	0.974	7.585	34.578
Pupa	0.0111x – 0.1522 (0.0012) (0.0260)	0.956	13.605	89.365
Total immature	0.0024x – 0.0301 (0.0001) (0.0038)	0.980	12.302	408.163

Numbers in the parentheses are SEM at each developmental stage.

Egg: $F_{1,4} = 107.83$, $P = 0.0005$; 1st: $F_{1,4} = 224.87$, $P = 0.0001$; 2nd: $F_{1,4} = 62.03$, $P = 0.0014$; 3rd: $F_{1,4} = 104.16$, $P = 0.0005$; 4th: $F_{1,4} = 102.41$, $P = 0.0005$; 5th: $F_{1,4} = 109.44$, $P = 0.0005$; 6th: $F_{1,4} = 102.12$, $P = 0.0005$; prepupa: $F_{1,4} = 147.67$, $P = 0.0003$; larva period: $F_{1,4} = 238.87$, $P < 0.0001$; pupa: $F_{1,4} = 86.69$, $P = 0.0007$; total immature: $F_{1,4} = 192.12$, $P = 0.0002$; DD: degree-days. The linear model is for the range of 15–27.5 °C. Larval period is combined from 1st instar to prepupa.

(SAS Institute, 2002) or TableCruve 2D (Jandel Scientific, 1994). The goodness-of-fit for the nonlinear equation was assessed by the adjusted coefficient of determination and the residual sum of squares. The lower developmental threshold and thermal constant were calculated by linear regression.

The relationships between the cumulative proportion of each life stage and the normalized developmental times were fitted by the two-parameter Weibull distribution function (Weibull, 1951; Wager et al., 1984) because the Weibull function could be applied in a wide variety of data analysis and prediction with small samples:

$$F(x) = 1 - \exp\left(-(x/a)^b\right),$$

where $F(x)$ is the cumulative frequency at normalized time x (developmental time / mean developmental time), a is the scale parameter, and b is the parameter of curve shape.

Selection of a model for simulation

The performance of linear and nonlinear models was evaluated by statistical information criteria based on the Akaike and Bayes–Schwarz information criteria (AIC and BIC, respectively) (Burnham and Anderson, 2002). It is indicated that the lower value of AIC and BIC is the preferred model. AIC_C was used instead of AIC because the sample size was small ($\frac{n}{p} < 40$):

$$AIC = n[\ln(RSS)] - [n - 2(p + 1)] - n\ln(n)$$

$$AIC_C = AIC + 2p(p + 1)/(n - p - 1)$$

$$BIC = n[\ln(RSS)] + (p + 1)\ln(n) - n\ln(n),$$

where n is the number of observation, RSS is the residual sum of squares and p is the number of parameters estimated.

The emergence of *C. medinalis* pupa and adults was simulated in relation to time (day) and constant temperature by combining the selected equation and the Weibull function. The rate of daily emergence at a given temperature was determined by the selected developmental rate model, and the cumulative frequency of pupae and adults was calculated using the Weibull distribution model:

$$F(x, T) = 1 - \exp\left(-(x r(T)/a)^b\right),$$

where $F(x, T)$ is the cumulative proportion of the emergence of *C. medinalis* pupae and adults at time x and constant temperature T , x is time (day), $r(T)$ is the selected developmental rate model, and a and b are parameters from the Weibull equation.

Validation of larval development

Eggs collected from the stock culture were allowed to hatch for 12 h, and 40 first-instar larvae were randomly selected. Using a small paint brush, the larvae were placed onto the leaves of potted rice plants (var. Chucheong). These experiments were conducted in the experimental field of the National Academy of Agricultural Science (NAAS) in Suwon, Korea, in late April, late June, and the middle of August of 2005. Each experiment was repeated three times. Temperature was recorded daily using Hobo data loggers (Hobo Temp-H08-001-02; Onset Computer Corp.). The development of the larvae was observed every 2 or 3 days until the larvae began folding the rice leaves. After folding the leaves, the growth of larvae was carefully examined every day, and the time of pupation was recorded.

Validation of adult emergence

Five virgin females and males were transferred from the stock culture to plastic containers (diameter \times height, 9.0 \times 5.0 cm). A sugar solution (10%) was supplied as a food source. A piece of water-saturated cotton was placed in the container to maintain the relative humidity. The mated females were allowed to lay eggs for 12 h on a piece of gauze that was placed inside the container. Fifty eggs were selected randomly from the egg stock and, using a small paint brush, were placed onto the leaves of potted rice plants (var. Chucheong). This experiment was conducted in the greenhouse of the National Academy of Agricultural Science (NAAS) in Suwon, Korea, in late May 2010. The greenhouse was maintained at 18–25 °C, 50 \pm 10% relative humidity, and a 16:8 h light:dark cycle. Temperature was also recorded daily using a Hobo data logger (Hobo H8 Pro Series; Onset Computer Corp.). The emergence of adults was observed every day after pupation. The relationships between the model predictions and the observed pattern of pupation and adult emergence were evaluated by calculating the coefficient of determination (r^2 values) for the relationships.

Results

Cnaphalocrocis medinalis developed successfully from egg to the adult stage at all temperatures tested (Table 1). Between 57% and 78% of eggs hatched at each temperature. The developmental time of *C. medinalis* decreased until the temperature reached 32.5 °C, and then times increased at temperatures above 32.5 °C. The developmental time for all immature stages combined was longest at 15 °C (115.6 \pm 3.51 days) and shortest at 32.5 °C (20.9 \pm 0.69 days). The developmental time of each immature stage was significantly influenced by temperatures (egg: $F_{8,1095} = 3488.12$, $P < 0.0001$; Larva, 1st instar: $F_{8,479} = 676.34$, $P < 0.0001$; 2nd instar: $F_{8,357} = 231.98$, $P < 0.0001$; 3rd instar: $F_{8,325} = 139.86$, $P < 0.0001$; 4th instar: $F_{8,350} = 100.20$, $P < 0.0001$; 5th instar: $F_{8,260} = 150.06$, $P < 0.0001$; 6th instar: $F_{8,260} = 150.06$, $P < 0.0001$).

Table 3Parameter estimates (\pm SEM) for three nonlinear developmental rate models for *Cnaphalocrocis medinalis*.

Equations	Parameters	Life stage										
		Egg	1st larva	2nd	3rd	4th	5th	6th	Larval period	Prepupa	Pupa	Total immature
Logan 6	Ψ	0.0238 (1.7745)	0.0364 (7.2244)	0.0306 (3.7201)	0.0446 (8.7896)	0.0665 (21.5301)	0.0672 (45.8636)	0.0925 (318.2808)	0.0080 (2.0935)	0.1537 (14.4950)	0.0094 (1.2501)	0.0256 (254.6173)
	ρ	0.1441 (0.7582)	0.1493 (1.4237)	0.1606 (1.1559)	0.1682 (1.2153)	0.1477 (1.8688)	0.1516 (2.8666)	0.1713 (5.3992)	0.14830 (1.4464)	0.1182 (0.7122)	0.1756 (1.0585)	0.1640 (6.9114)
	T_M	41.5111 (4.3277)	39.8248 (3.5661)	39.6531 (3.2976)	37.7526 (1.0831)	38.7377 (2.6636)	38.2408 (2.4691)	37.6132 (1.2491)	39.0119 (2.1894)	39.4014 (1.8875)	38.0540 (1.2951)	39.2746 (1.4766)
	ΔT	6.2527 (36.7720)	6.1999 (63.0383)	5.6926 (44.4617)	5.5934 (41.9731)	6.3427 (83.7050)	6.2816 (122.1662)	5.7354 (182.6327)	6.3334 (64.5067)	7.6443 (48.3695)	5.2988 (33.6573)	6.0457 (256.4733)
	r^2	0.9886	0.9678	0.9737	0.9739	0.9401	0.9149	0.9575	0.9692	0.9686	0.9787	0.9912
	RSS	0.0011	0.0038	0.0075	0.0061	0.0098	0.0094	0.0041	7.5e–05	0.0046	0.0007	1.6e–05
	Adj r^2	0.9772	0.9356	0.9475	0.9479	0.8803	0.8298	0.9151	0.9384	0.9372	0.9574	0.9825
Briere 1	a	0.0001 (2.1e–05)	0.0002 (2.2e–05)	0.0002 (4.9e–05)	0.0003 (4.2e–05)	0.0002 (3.8e–05)	0.0002 (3.8e–05)	0.0002 (3.7e–05)	3.1e–05 (3.2e–06)	0.0002 (3.2e–05)	0.0001 (1.3e–05)	2.2e–05 (2.3e–06)
	T_L	9.0725 (1.5046)	10.7210 (1.1310)	11.6146 (1.5139)	12.1160 (1.1533)	10.3994 (1.4947)	10.8751 (1.7015)	11.8524 (1.5982)	10.1389 (1.0873)	2.9401 (2.2196)	13.0996 (0.9559)	11.0273 (0.9044)
	T_M	49.5001 (4.6275)	41.2185 (1.3869)	43.2196 (2.9177)	37.9622 (0.7622)	38.5514 (0.9594)	37.8032 (0.9180)	37.7384 (0.9490)	39.2895 (0.8226)	38.6639 (0.7146)	39.0814 (0.9910)	41.5743 (1.2296)
	r^2	0.9925	0.9878	0.9794	0.9713	0.9689	0.9496	0.9459	0.9861	0.9758	0.9807	0.9920
	RSS	0.0007	0.0014	0.0059	0.0068	0.0051	0.0055	0.0053	3.4e–05	0.0035	0.0006	1.4e–05
	Adj r^2	0.9881	0.9805	0.9671	0.9541	0.9502	0.9195	0.9134	0.9778	0.9613	0.9692	0.9872
	m	0.0161 (0.0015)	0.0226 (0.0056)	0.0295 (0.0040)	0.0319 (0.0043)	0.0324 (0.0110)	0.0282 (0.0113)	0.0208 (0.0038)	0.0034 (0.0006)	0.0320 (0.0077)	0.0112 (0.0014)	0.0024 (0.0001)
Shi	T_{Min}	11.8915 (0.9245)	12.7111 (1.0035)	12.9316 (1.1732)	12.6394 (1.1483)	12.5540 (1.4133)	12.9015 (1.5758)	12.3991 (1.5749)	12.0489 (1.1007)	8.2947 (2.0467)	13.5665 (0.9724)	12.2097 (0.6249)
	K	0.4984 (8.7594)	0.1420 (0.2040)	0.4498 (1.1591)	0.3942 (0.2852)	0.1400 (0.1621)	0.13923 (0.1667)	0.3892 (0.3495)	0.1957 (0.1663)	0.1739 (0.1270)	0.4085 (0.3813)	0.8115 (0.9535)
	T_{Max}	44.1249 (153.2772)	45.2868 (10.6783)	40.0251 (11.9042)	37.7014 (1.7388)	41.6253 (5.1475)	40.5819 (4.4231)	37.5748 (2.0555)	41.0592 (3.9198)	40.5009 (2.8104)	38.2782 (2.7384)	37.3242 (2.5966)
	r^2	0.9888	0.9879	0.9759	0.9710	0.9677	0.9489	0.9480	0.9834	0.9726	0.9772	0.9924
	RSS	0.0011	0.0014	0.0069	0.0069	0.0053	0.0056	0.0051	4.1e–05	0.0041	0.0007	1.3e–05
	Adj r^2	0.9776	0.9760	0.9519	0.9421	0.9354	0.8979	0.8959	0.9667	0.9452	0.9543	0.9848

Numbers in the parentheses are SEM at each developmental stage.

Logan 6: Egg: $F_{3,5} = 144.76$, $P = 0.00003$; 1st: $F_{3,5} = 50.12$, $P = 0.00037$; 2nd: $F_{3,5} = 61.89$, $P = 0.00022$; 3rd: $F_{3,5} = 62.34$, $P = 0.00022$; 4th: $F_{3,5} = 26.17$, $P = 0.00175$; 5th: $F_{3,5} = 17.93$, $P = 0.00416$; 6th: $F_{3,5} = 37.60$, $P = 0.00074$; prepupa: $F_{3,5} = 51.42$, $P = 0.00035$; larval period: $F_{3,5} = 52.45$, $P = 0.00034$; pupa: $F_{3,5} = 76.72$, $P = 0.00013$; total immature: $F_{3,5} = 189.66$, $P = 0.00001$; Briere 1: Egg: $F_{2,6} = 400.03$, $P < 0.00001$; 1st: $F_{2,6} = 243.78$, $P < 0.00001$; 2nd: $F_{2,6} = 142.89$, $P = 0.00001$; 3rd: $F_{2,6} = 104.45$, $P = 0.00002$; 4th: $F_{2,6} = 93.49$, $P = 0.00003$; 5th: $F_{2,6} = 56.59$, $P = 0.00013$; 6th: $F_{2,6} = 52.47$, $P = 0.00016$; prepupa: $F_{2,6} = 121.22$, $P = 0.00001$; larval period: $F_{2,6} = 213.183$, $P = 0.00001$; pupa: $F_{2,6} = 152.80$, $P = 0.00001$; total immature: $F_{2,6} = 373.58$, $P < 0.00001$.

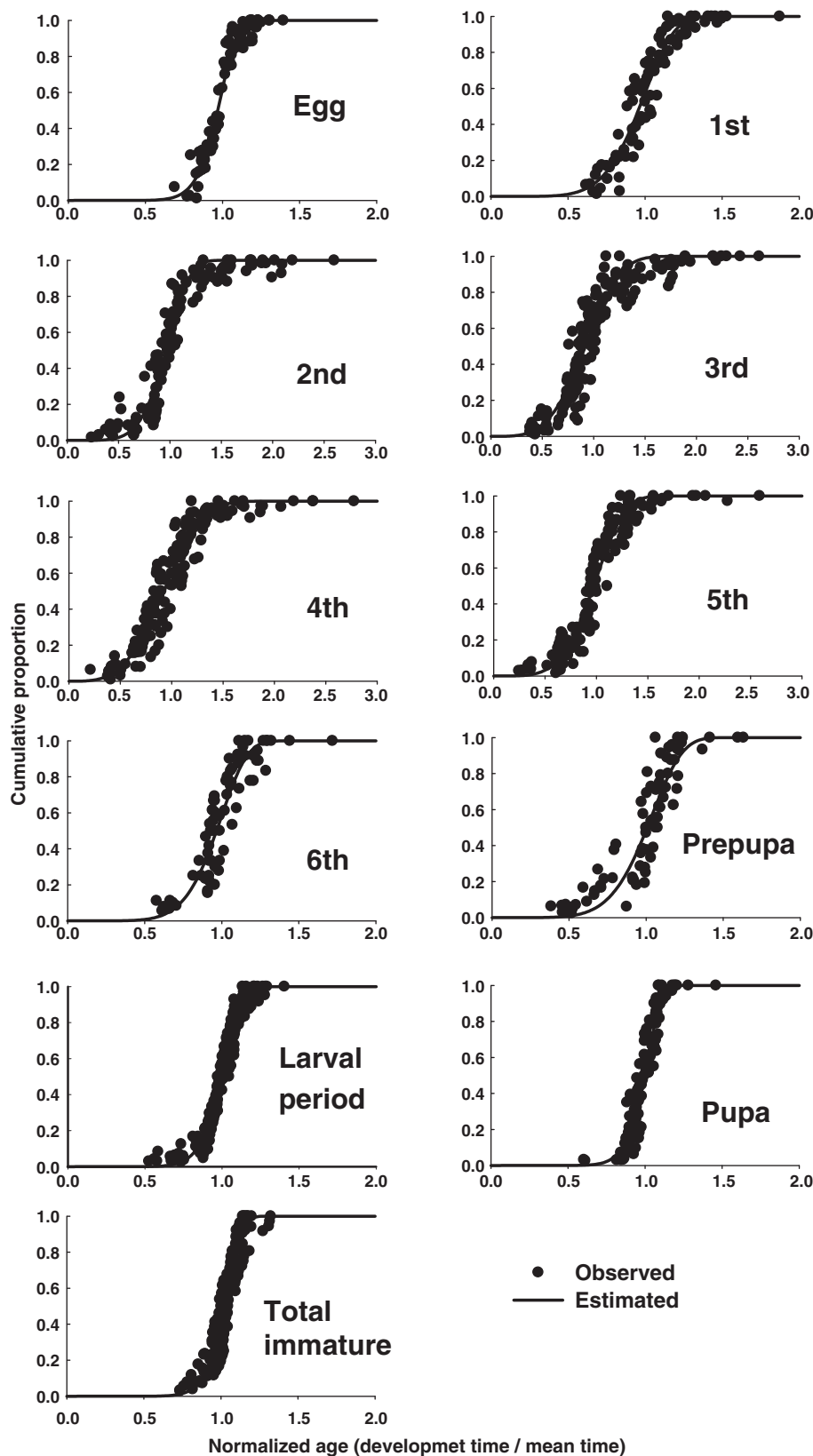


Fig. 2. Cumulative proportions of development completion for each stage of *Cnaphalocrocis medinalis* as a function of normalized time (developmental time/mean developmental time). Fitted curve: the two-parameter Weibull function (solid line). Solid dots are observed data.

$_{122} = 178.79$, $P < 0.0001$; prepupa: $F_{8, 228} = 72.69$, $P < 0.0001$; pupa: $F_{8, 230} = 1187.95$, $P < 0.0001$; all immature stages combined: $F_{8, 179} = 835.24$, $P < 0.0001$). The total mortality of immature *C. medinalis* was lowest at 25 °C and highest at 35 °C.

The relationship between the developmental rates of each stage of *C. medinalis* and temperatures was described using linear and nonlinear functions (Fig. 1). The parameters, lower developmental thresholds, and thermal constants were calculated using linear regression (Table 2).

Table 4
Estimated parameters of Weibull function for *Cnaphalocrocis medinalis*.

Life stage	Parameter		r^2	F value	P value
	a	b			
Egg	1.0031 ± 0.0032	10.5263 ± 0.4770	0.963	1984.64	P < 0.0001
1st larva	1.0260 ± 0.0065	6.1120 ± 0.3708	0.917	997.71	P < 0.0001
2nd	1.0274 ± 0.0063	5.7348 ± 0.3306	0.932	1766.02	P < 0.0001
3rd	1.0116 ± 0.0096	3.8442 ± 0.2391	0.878	1069.6	P < 0.0001
4th	1.0266 ± 0.0083	3.5166 ± 0.1532	0.923	1829.30	P < 0.0001
5th	1.0536 ± 0.0066	4.5793 ± 0.1977	0.934	2036.43	P < 0.0001
6th	1.0191 ± 0.0084	6.8307 ± 0.6622	0.835	359.45	P < 0.0001
Larval period	1.0364 ± 0.0016	10.6033 ± 0.2806	0.9601	4626.41	P < 0.0001
Prepupa	1.0676 ± 0.0102	6.2545 ± 0.6828	0.834	361.89	P < 0.0001
Pupa	1.0263 ± 0.0033	12.1200 ± 0.6499	0.906	972.85	P < 0.0001
Total immature	1.0664 ± 0.0029	11.8810 ± 0.5965	0.880	1034.07	P < 0.0001

The lower developmental thresholds were estimated to be 11.97, 11.98, 13.61, and 12.30 °C for egg, larva, pupa, and the immature stages combined, respectively (egg: $F_{1,4} = 107.83$, $P = 0.0005$; larval period: $F_{1,4} = 238.87$, $P < 0.0001$; pupa: $F_{1,4} = 86.69$, $P = 0.0007$; combined immature stages: $F_{1,4} = 192.12$, $P = 0.0002$). The thermal constants of egg, larva, pupa, and combined immature stages based on lower developmental threshold were 61.39, 296.74, 89.37, and 408.16 degree-days (DD), respectively.

The estimated parameter values of the nonlinear developmental models are presented in Table 3. The nonlinear shape of the temperature-dependent development was well described by three functions (Fig. 1). The residual sum of square of the Briere 1 model was lower than that of other models except for in the 3rd and 6th instar larval stages. The lower developmental thresholds estimated by linear regression were higher than those estimated by the Briere 1 models. Developmental completion of each stage of *C. medinalis* was described using a two-parameter Weibull distribution model (Fig. 2 and Table 4). The developmental completion of *C. medinalis* larva ($b = 10.60$) was wider than that of pupa ($b = 12.12$); the lower value of b parameter means the higher variability of distribution.

The statistical information criteria of the four temperature-dependent developmental models are presented in Table 5. The Briere 1 model showed the lowest values of AIC_C and BIC. It was determined that the performance of the Briere 1 model was better than that of other functions and showed a higher degree of fit. The emergence of *C. medinalis* adults over the full range of constant temperatures (14–40 °C) was expressed by the simulation model (Fig. 3). The developmental times of *C. medinalis* larvae decreased until the temperature reached 35 °C, and then increased at temperatures above 35 °C. The performance of the simulation model differed when using the two nonlinear functions (Fig. 3).

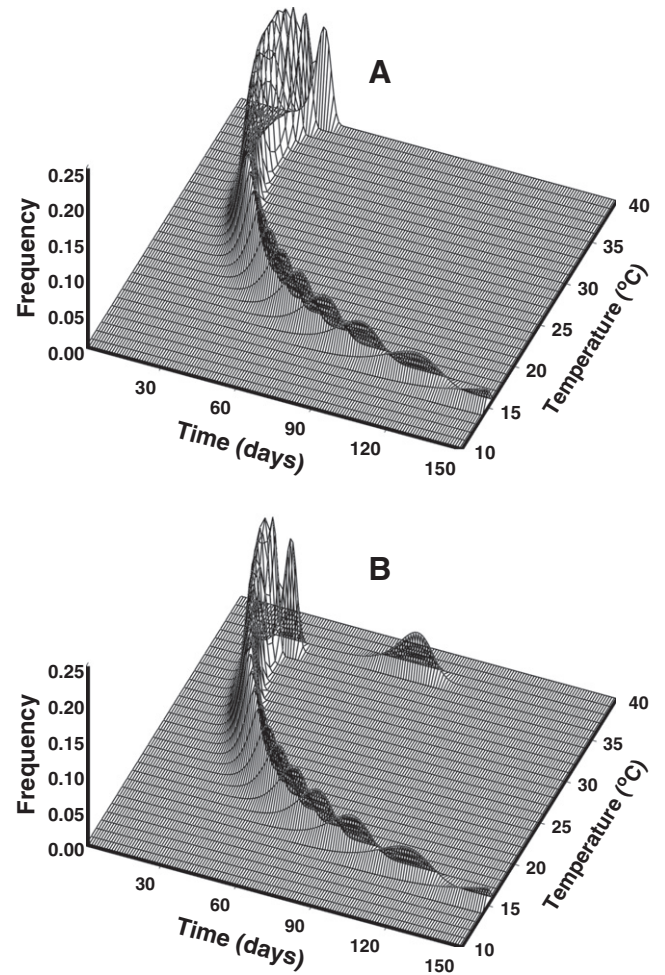


Fig. 3. Simulated temperature-dependent emergence of *Cnaphalocrocis medinalis* adults: (A) simulated by using the Briere 1 model and (B) simulated by using the Shi et al. model.

The observed and estimated values of larval development (pupation) are presented in Fig. 4A. The pattern of pupa occurrence from the semi field was well described by the Briere 1 model ($r^2 = 0.93$, 0.95, and 0.94, respectively). The estimated and observed values of adult emergence are presented in Fig. 4B. The occurrence of *C. medinalis* adults started on the 35th day. The observed and estimated cumulative 50% occurrence times of *C. medinalis* adults were on the 38th day. The pattern of adult occurrence under greenhouse conditions was also well described by the Briere 1 model ($r^2 = 0.99$).

Table 5
Values of statistical model selection criteria of three models for the relationship between temperature and development rate of *Cnaphalocrocis medinalis*.

SIC ^a	Function	Life stage										
		Egg	1st larva	2nd	3rd	4th	5th	6th	Larval period	Prepupa	Pupa	Total immature
AIC _C ^b	Logan 6	−70.038	−58.869	−52.761	−54.565	−50.340	−50.768	−58.031	−94.140	−57.134	−74.165	−108.158
	Briere 1	−81.060	−74.831	−62.149	−60.884	−63.437	−62.689	−63.050	−108.514	−66.694	−82.257	−116.163
	Shi	−70.173	−67.742	−53.544	−53.604	−55.899	−55.359	−56.193	−99.680	−58.364	−73.519	−109.374
	Linear	−47.735	−48.932	−36.911	−40.031	−40.478	−42.441	−45.491	−68.972	−42.748	−50.951	−73.935
BIC ^c	Logan 6	−70.052	−58.883	−52.775	−54.579	−50.354	−50.782	−58.045	−94.154	−57.148	−74.179	−108.172
	Briere 1	−76.071	−69.842	−57.160	−55.895	−58.448	−57.700	−58.061	−103.526	−61.705	−77.268	−111.173
	Shi	−70.187	−67.756	−53.558	−53.618	−55.913	−55.373	−56.207	−99.694	−58.378	−73.533	−109.388
	Linear	−46.360	−47.556	−35.536	−38.656	−39.103	−41.066	−44.115	−67.597	−41.372	−49.576	−72.560

Larval period: from 1st larva to total immature.

^a Statistical information criteria.

^b Akaike information criterion.

^c Bayes–Schwarz information criterion.

Discussion

The developmental time and mortality of *C. medinalis* were significantly affected by temperature, as in other insects (Park et al., 2010a, 2010b; Han et al., 2013; Wang et al., 2013). The total developmental time of the immature stages of *C. medinalis* was not significantly different among high temperatures (27.5–35 °C). The results at 27.5–35 °C were similar to those for the Japanese population (Kyushu strict) (Wada and Kobayashi, 1980); however, those for the Indian population (35.23 days) were longer than that in both countries at 30–32 °C (Velusamy and Surbramaniam, 1974). Egg periods in our study were longer than those of the Japanese population at each temperature, except at 15 °C. The larval periods of our study were longer than those of the Japanese population because the Japanese study excluded the period of the 6th and 7th instars when calculating the larval period. The developmental periods of larva *C. medinalis* fed on artificial diet and rice leaf in China was longer than those of our study except 5th instar at 25 °C (Xu et al., 2012). There was no difference on pupal duration (8.4 days) between both populations when larvae consumed on rice leaf. However, the pupal period (10.1 days) of larva fed on artificial diet in China was higher than that of our study.

In contrast to our study, Wada and Kobayashi (1980) described the relationship between the developmental rate and temperature for *C. medinalis* using only linear regression. Furthermore, in our study, the lower development thresholds estimated by the linear regression of each life stage and combined immature stages were lower than those of the Japanese population. It can be inferred because the collection latitude (33°43'N 130°69'E) of the Japanese populations was lower than that of the Korean populations. The thermal constants of our results were longer than those of the Japanese population at each life stage because the thermal constant was calculated by inverting the slope of the linear equation. It may be interpreted that the Japanese population is more sensitive to temperature than the Korean population. The higher development threshold (between 30 and 35 °C) of *C. medinalis* from Heong et al. (1995) was lower than that of our study.

The developmental rate of *C. medinalis* was well fitted by three non-linear models and lethal thresholds were calculated using the models (Fig. 1 and Table 3). The values of lower developmental threshold estimated by the Briere 1 model were lower than those of the Shi et al. model and linear equation. The nonlinear performance of the temperature development of *C. medinalis* was fitted best by the Briere 1 model and it was supported by statistical criterion information (Table 5).

Cnaphalocrocis medinalis is a migratory rice pest in Korea. Sporadic and serious outbreaks of *C. medinalis* have been reported in many Asian countries (Islam and Karim, 1997; Park et al., 2010a, 2010b; Padmavathi et al., 2013). Therefore, understanding the migratory process and spread pathways of *C. medinalis* is important in developing an effective management strategy and to improve the monitoring system. Although a part of the functional transcriptome and the population genetics of *C. medinalis* was reported (Wan et al., 2011; Li et al., 2012), spatio-temporal analysis of *C. medinalis* populations will be necessary to establish a control method and to interpret the dispersal process.

In conclusion, temperature-dependent developmental models for *C. medinalis* can be used to predict the emergence of each life stage of *C. medinalis*, to establish a management strategy for *C. medinalis*, and to develop a population phenology model for *C. medinalis*.

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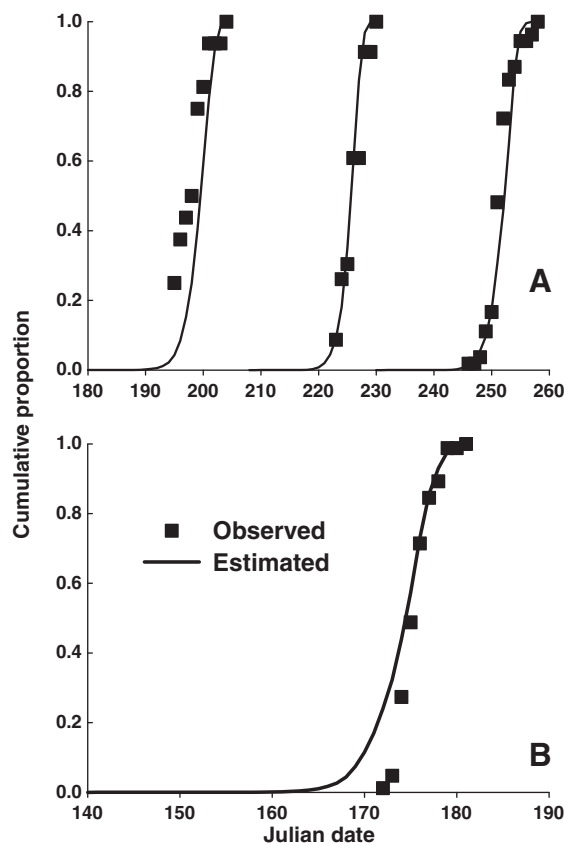


Fig. 4. Comparison between observed and estimated values of emerging *Cnaphalocrocis medinalis* (A) for pupa and (B) for adult. Fitted curve: the Briere 1 equation (solid line). Solid dots are observed data.

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